INVERSE DENSITY-DEPENDENT PARASITISM OF *OPSIUS STACTOGALUS* FIEBER (HOMOPTERA: CICADELLIDAE) BY *GONATOPUS* SP. (HYMENOPTERA: DRYINIDAE)

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Abstract.—The relationship between *Opsius stactogalus* Fieber leafhopper density (abundance per plant-sample mass) and parasitism by the dryinid wasp *Gonatopus* sp. was examined. Branches cut from *Tamarix ramosissima* Ledebour shrubs, sustained by treated wastewater, were weighed and sampled for parasitized and unparasitized leafhoppers. Leafhopper abundance increased linearly as branch mass increased exponentially (mass$^{0.64}$), in agreement with isometric scaling laws relating leaf abundance to branch mass. The proportion of leafhopper nymphs parasitized (18%) was greater than the proportion of adults parasitized (2.9%). Branches were more likely to contain one or more parasitized nymphs, signifying exploitation of the branch by *Gonatopus*, as nymph density increased. On branches containing at least one parasitized nymph, increasing nymph density was related to an increase in the number of parasitized nymphs but to a decrease in parasitism rate. Parasitism of *O. stactogalus* nymphs on branches exploited by *Gonatopus* was inverse density dependent. *Gonatopus* appears not to regulate populations of *O. stactogalus* or limit the leafhopper's damage to *T. ramosissima*.

Key Words.—Insecta, Cicadellidae, *Opsius stactogalus*, Dryinidae, *Gonatopus*, *Tamarix*, parasitism.

The tamarix leafhopper, *Opsius stactogalus* Fieber, is a small, cryptic insect primarily found on tamarisk, *Tamarix* spp. (Tamaricaceae) (Harding 1930, Liesner 1971). Tamarisk is a halophytic shrub or tree facultatively-dependent on shallow groundwater (Brock 1994, Di Tomaso 1998). Species of *Tamarix* are native to the Old World, occurring from the Mediterranean across southern Russia to eastern Asia, and were imported to the USA in the early 1800s for use as ornamentals (Robinson 1965). Tamarisk since has spread beyond cultivation with the most-recent survey estimating the plant's extent to exceed 350,000 ha in the western USA (Robinson 1965). Tamarisk's invasiveness, water uptake, and low diversity of dependent wildlife has made it the target of classical biological control (Fornasari 1997). The taxonomy of New World *Tamarix* is unclear (Brock 1994, Di Tomaso 1998); eight species occur in North America (Baum 1967) with five species, four deciduous and one evergreen, currently recognized in California (Wilken 1993).

Opsius stactogalus is the most abundant insect on tamarisk (Harding 1930, Hopkins & Carruth 1954, Liesner 1971). The insect's green color and size (length 0.81 mm for first-instar nymphs, 4.5 mm for adult females, Harding 1930) make it difficult to distinguish from tamarisk's sessile, scalelike leaves (1.5 to 3.5 mm-long in *Tamarix ramosissima* Ledebour, Wilken 1993). The life cycle of *O. stactogalus* is comprised of five nymphal instars, adults, and eggs inserted within stems (Harding 1930). Generations per year number three in Kansas (Harding 1930) and four in New Mexico (Liesner 1971). Like many other Cicadellidae, *O. stactogalus* is a fluid-feeder, and the aggregate feeding imposed by populations of the leafhopper can reduce tamarisk's growth (Liesner 1971). Although the

leafhopper was described as a new species in 1907 from collections in Texas, a later comparison of Meditteranean and North American specimens and review of the systematic literature revealed the 1907 species description as synonymous with an original description in Europe during 1847 (Harding 1930). *Opsius stactogalus*, like its host tamarisk, is native to the Old World.

Opsius stactogalus nymphs and adults are parasitized by the dryinid wasp *Gonatopus* spp. (Harding 1930, Liesner 1971). Dryinidae occur worldwide and parasitize only the homopteran suborder Auchenorrhyncha (Olmi 1984). Dryinid larvae are individually enclosed in a sac of exuviae that protrudes between their host's thoracic or abdominal sclerites. Adult females of many Dryinidae species also are predaceous on their hosts (Olmi 1984). The only published records of *Gonatopus* parasitizing *O. stactogalus* in North America are of *Gonatopus caroli* Olmi and *Gonatopus curriei* Krombein (Guglielmino & Olmi 1997). One adult female *Gonatopus* reared from a parasitized *O. stactogalus* I collected at the present study's locality was identified as *G. caroli* (M. Olmi, personal communication).

The effect of parasitism by *Gonatopus* on the abundance of *O. stactogalus* is uncertain. Harding (1930) described parasitism rate by *Gonatopus* as low and unable to significantly affect rapid population increases of *O. stactogalus*. In contrast, Liesner (1971) described parasitism rates (30–44% of leafhoppers parasitized) high enough to hinder his collecting leafhoppers for experimental trials. Increasing parasitism rate with increasing *O. stactogalus* density (density dependence) may regulate leafhopper populations (Turchin 1995) and decrease their detrimental effect on tamarisk. Parasitism rate decreasing with increasing leafhopper density (inverse density dependence) or unrelated to leafhopper density (density independence) would not regulate populations of *O. stactogalus* and limit the insect's damage to tamarisk. A synopsis (Stiling 1987) of the relationships between insect-host density and parasitism rate (171 published accounts) found density independence most common (52%) followed by density dependence (25%) and inverse density dependence (23%). This study examines the relationship between density of *O. stactogalus* and parasitism rate by *Gonatopus*.

MATERIALS AND METHODS

The study site was located at the effluent discharge of the City of Boulder City, Clark County, Nevada, wastewater treatment plant. The treatment plant discharges approximately 2000 m^3 of secondary-treated municipal effluent per day equally into two parallel unlined southward-flowing channels approximately 0.1 km apart. Effluent discharged to each channel maintains a 2-m wide surface flow extending approximately 3 km downstream. Sustained by the effluent, and bordering both channels, are dense, linear stands of the deciduous tamarisk *T. ramosissima* alternating with clumps of cat-tail, *Typhus latifolia* L. (Typhaceae). The site lies at an elevation of 610 m within the Mojave Desert; creosote bush, *Larrea tridentata* (Sessé & Mocino ex Candolle) Coville (Zygophyllaceae), and bursage, *Ambrosia dumosa* (Gray) Payne (Asteraceae), are the dominant plant species surrounding the effluent-supported vegetation.

Leafhoppers on tamarisk were sampled at 12 points along the west edge of the east channel. Sampling points were located every 80 m along the channel beginning 80 m downstream of the effluent discharge. Three samples were taken at

each point during the morning on 17–18 Jul, 16–17 Aug, 16–17 Sep, and 20–21 Oct 1999. Each leafhopper sample was taken by bagging a 1-m long tamarisk branch within a plastic trash bag (159 liter, 84 cm × 1.2 m, 76 μm thick) held open with a 52-cm diameter metal hoop. The bag was quickly swept over the branch and slipped off the hoop to constrict the bag around the proximal-end of the branch. The branch then was cut at the top of the bag, pushed into the bag, and the bag closed. Enclosed leafhoppers were killed with an aerosol insecticide (Raid® Concentrated Deep Reach Fogger, S.C. Johnson & Son, Racine, Wisconsin) containing 14 g of 1.7% cypermethrin. Approximately 10 min after treatment, the bag was held upright and the branch shaken for 30 sec. Dead leafhoppers shaken from the branch were collected into a 3-dram (15-mm diameter × 65-mm long) patent-lip glass vial. Plant mass supporting the collected leafhoppers was measured (± 2 g) by removing the branch from the bag and weighing it with a 300-g capacity spring scale. Vial contents were examined with a microscope, and collected leafhoppers were sorted from plant debris and stored in 70% ethanol. Leafhoppers were examined at 30× and the number of parasitized and unparasitized nymphs and adults counted. Parasitized and unparasitized *O. stactogalus* in ethanol were deposited as vouchers at the University of California, Riverside, Entomology Museum.

Opsius stactogalus density was estimated by first determining the relationship between leafhopper abundance and plant mass. Leafhopper abundance (transformed $\ln[Y + 0.5]$) was regressed (SPSS version 6.1, Chicago, Illinois) against plant mass and life stage, nymph or adult coded as an indicator variable. Two regressions were performed with plant mass in grams and with plant mass transformed ln(grams). Plant mass transformed ln(grams) was selected, due to its greater partial r^2, as the better linear predictor of leafhopper abundance and used to calculate leafhopper density. The interaction life stage × plant mass was added to the regression to test if the trends in abundance across transformed plant mass differed between nymphs and adults. For graphing, abundances of nymphs and adults in each sample were summed, transformed $\ln(Y + 0.5)$, and regressed against transformed plant mass.

Parasitism of *O. stactogalus* was examined by first comparing (χ^2 test) the proportions of parasitized nymphs and adults. Parasitism of nymphs was further examined at two spatial scales, the tamarisk branch and the individual leafhopper. To evaluate exploitation of tamarisk branches by ovipositing *Gonatopus,* the influence of nymph density ($\ln[N + 0.5]/\ln[g]$; N = number of nymphs, g = grams plant mass) on the probability of a leafhopper sample containing at least one parasitized nymph was determined with logistic regression (Neter et al. 1996). A predicted change and 95% confidence interval in the odds of a *Gonatopus* exploiting versus not exploiting a branch as nymph density increased was calculated from the regression coefficient and its standard error.

To evaluate parasitism of individual leafhoppers on branches exploited by *Gonatopus,* the number of parasitized nymphs (G) in leafhopper samples with at least one parasitized nymph was transformed $\ln(G + 0.5)$ and regressed against nymph density. One outlier leafhopper sample, collected on 17 Aug 1999, containing 35 unparasitized nymphs and 41 parasitized nymphs was excluded from the regression due to its extreme influence (standardized residual = 3.4) on the fitted function. Parasitism rate (R) on branches exploited by *Gonatopus* was quantified as
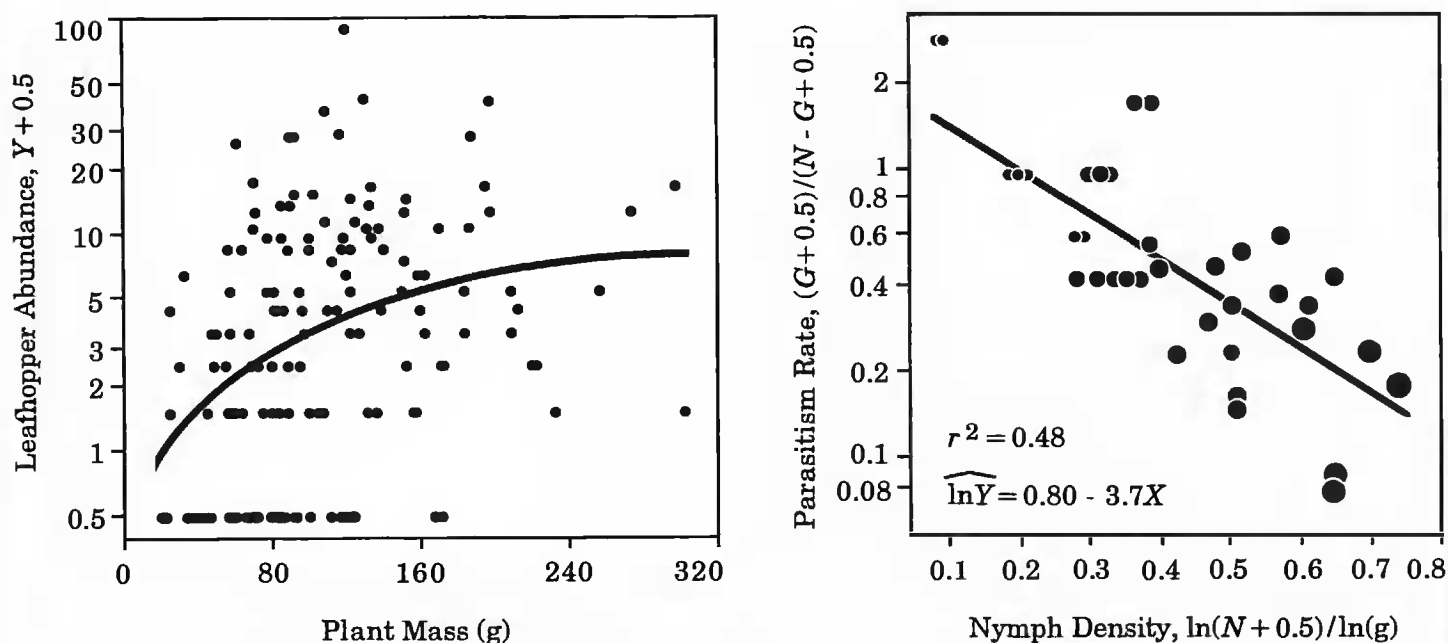
Figures 1–2. Fig. 1 (left). *Opsius stactogalus* abundance (nymphs + adults) plotted on a logarithmic scale against *Tamarix*-branch mass. Curve was fit by linear regression with plant mass transformed ln(g). Fig. 2 (right). Parasitism rate of *O. stactogalus* nymphs versus nymph density (N = nymph abundance) on exploited branches containing $\geq$ 1 parasitized nymph. Parasitism rate is the ratio of parasitized nymphs (G) to unparasitized nymphs plotted on a logarithmic scale. The size of each data point represents its final weight determined from iteratively reweighted least squares regressions.

the ratio of the number of parasitized nymphs to the number of unparasitized nymphs ($N - G$), transformed as an empirical logit (Agresti 1990), $R = \ln[(G + 0.5)/(N - G + 0.5)]$ in each leafhopper sample. Iteratively reweighted least squares regressions (see logistic regression with repeat observations, Neter et al. 1996) of parasitism rate against nymph density were performed to produce a maximum likelihood estimate of the regression coefficient. The regression was unweighted in the first iteration, and the resulting predicted parasitism rates ($\hat{R}$) were used to calculate predicted probabilities of parasitism, $\pi = [\exp(\hat{R})]/[1 + \exp(\hat{R})]$. A weighted regression then was performed with leafhopper-sample weights calculated with $N(\pi)(1 - \pi)$. Predicted probabilities of parasitism from the weighted regression were used to recalculate weights, and the process was repeated (3 iterations) until the regression coefficient stabilized. Weights determined in the final iteration were adjusted downward (multiplied by 34/51) to restore the unweighted error degrees of freedom. The leafhopper sample identified above as an outlier again was excluded (standardized residual = 3.2) from the analysis. A predicted change in the odds ratio of parasitized nymphs (+ 0.5) to unparasitized nymphs (+ 0.5) as nymph density increased was calculated from the regression coefficient.

RESULTS

Abundance of *O. stactogalus* was more linearly related to plant mass transformed ln(grams) (partial r^2 = 0.092; F = 29.8; df = 1,285; P < 0.001) (Fig. 1) than to plant mass in grams (partial r^2 = 0.065; F = 20.5; df = 1,285; P < 0.001) and was greater (F = 9.1; df = 1,285; P = 0.003) in nymphs (634 leafhoppers) than in adults (309 leafhoppers). The partial regression coefficient (0.64 ± 0.12 [SE]) for transformed plant mass therefore equaled the exponent of the power function, leafhopper abundance = f (plant mass$^{0.64}$). Trends in abundance

across transformed plant mass did not differ ($F = 0.47$; df $= 1,284$; $P = 0.5$) between nymphs and adults.

The proportion of *O. stactogalus* nymphs parasitized (18.0%) by *Gonatopus* was greater ($\chi^2 = 41.6$; df $= 1$; $P < 0.001$) than the proportion of adults parasitized (2.9%). Tamarisk branches supporting nymphs (99 of 144 total samples) were more likely ($\chi^2 = 41.4$; df $= 1$; $P < 0.001$) to be exploited by *Gonatopus* as nymph density increased. The odds of an ovipositing *Gonatopus* exploiting versus not exploiting a tamarisk branch increased 2.3-fold (95% confidence interval $= 1.8$ to 3.0) for a 2-fold increase, from 2 to 4 nymphs on a 100 g branch, in nymph density. The increase in the odds of *Gonatopus* exploiting a branch therefore was approximately proportional to the increase in nymph density.

On branches supporting at least one parasitized nymph (36 samples excluding outlier), increasing nymph density was related to an increase in the number of parasitized nymphs ($F = 15.6$; df $= 1,34$; $P = 0.004$) but to a decrease in the parasitism rate of nymphs ($F = 30.9$; df $= 1,34$; $P < 0.001$) (Fig. 2). The odds of a nymph being parasitized versus unparasitized decreased 38% with a 2-fold increase, from 2 to 4 nymphs on a 100 g branch, in nymph density. Parasitism of *O. stactogalus* nymphs on branches exploited by *Gonatopus* therefore was inverse density dependent.

DISCUSSION

A diminishing rate of increase in *O. stactogalus* abundance, as the mass of the tamarisk branch supporting the population increased, is predicted by the scaling laws of isometric growth (Schmidt-Nielsen 1984). Tamarisk branches cut for leafhopper samples were composed of a central, non-photosynthetic stem supporting smaller, branching stems covered with sessile leaves. The central stem contained vascular tissue transporting xylem and phloem to and from the leaves, the portion of the branch supporting *O. stactogalus*. The capacity for this transport, limiting the abundance of leaves (and leafhoppers) supported by the stem, would have been proportional to the area of the stem's cross-section. The mass of the stem, however, would have been proportional to its volume. As the stem grew, its cross-sectional area (A) would have increased more slowly than its mass (M) according to the equation $A = M^{2/3}$ or $A = M^{0.67}$. This function approximates the observed relationship between *O. stactogalus* abundance and tamarisk-branch mass.

Greater parasitism of nymphs compared to adults, as observed in *O. stactogalus*, also has been reported in other leafhopper species. Dryinids parasitizing eight species of leafhoppers inhabiting forage grass generally were found to attack nymphs more than adults (Buntin 1989). In contrast, Liesner (1971) observed higher rates of parasitism by *Gonatopus* in *O. stactogalus* adults (14–100%) than in nymphs (5–54%). Greater parasitism of *O. stactogalus* nymphs compared to adults is not due to different durations, and therefore exposure times, of the two life stages; both first through fifth instar nymphs and adults live an average of 1 month (Harding 1930). *Gonatopus* parasitizing *O. stactogalus* preferred nymphs over adults for hosts.

Increasing *O. stactogalus* nymph density was associated with increasing probability of a branch being exploited by *Gonatopus* and with increasing abundance of parasitized nymphs. *Gonatopus* therefore appears to be attracted to, or arrested by (Vinson 1984), populations of *O. stactogalus*. The increase in abundance of

parasitized nymphs, however, did not keep pace with the increase in nymph abundance, resulting in a parasitism rate that decreased as nymph density increased. Reproductive rates of parasitoids can lag behind those of their hosts due to lower fecundities or long host-handling times (Stiling 1987).

Inverse density-dependent parasitism of *O. stactogalus* by *Gonatopus* is contrary to most insect host-parasite systems that have been studied (Stiling 1987). Decreasing parasitism rate with increasing host density may be common in Dryinidae, however, as it also has been observed in several dryinid species parasitizing grassland leafhoppers (Waloff 1975). The only other insect known to parasitize *O. stactogalus* in North America is the egg parasite *Polynema saga* (Girault) (Hymenoptera: Mymaridae) (Lawson 1929). Harding (1930) found approximately 25% of *O. stactogalus* eggs in Kansas parasitized by *P. saga,* and Liesner (1971) dissected *P. (Barypolynema) saga* from the leafhopper's eggs in New Mexico. *Opsius stactogalus* therefore supports two parasite species separately attacking nymphs and adults or attacking eggs. In comparison, 34 of 50 cicadellid species collected in Kansas grasslands supported two or more species of parasites infecting nymphs and adults (Baldridge & Blocker 1980), and eggs of the leafhopper *Circulifer tenellus* (Baker) in Iran were found to harbor seven species of parasites (Walker et al. 1997). Although caged *O. stactogalus* were eaten by Chrysopidae larvae (Harding 1930) and spiders (Liesner 1971), and leafhoppers may be eaten by adult female *Gonatopus,* the contribution of predation to *O. stactogalus* mortality in nature is unknown. Inverse density-dependent parasitism of *O. stactogalus* by *Gonatopus* may not only be due to intrinsic differences between the two species, such as fecundity rate, but also to interactions across several trophic levels (Hare 1992). The leafhopper's abundant, predictable food source and low diversity of natural enemies may combine to increase its reproductive rate beyond that of its parasite.

Populations of *O. stactogalus* are not regulated (Turchin 1995) by the inverse density-dependent parasitism imposed by populations of *Gonatopus.* Unconstrained population increase by *O. stactogalus* agrees with descriptions (Harding 1930, Hopkins & Carruth 1954, Liesner 1971) of the leafhopper occurring on tamarisk in high densities. Liesner (1971) also suggested populations of *O. stactogalus* can be high enough to reduce tamarisk growth. Reduced growth expectedly would result from the photosynthate drain imposed on the plant by high densities of the fluid-feeding leafhopper. Lack of population regulation by *Gonatopus* permits unhindered herbivory by *O. stactogalus,* considered beneficial when viewed in the context of biological control against tamarisk. Populations of *O. stactogalus* and herbivory by the leafhopper may be limited only by temperature. Insect development and photosynthate extraction would slow during the fall as temperatures decline and would cease when *T. ramosissima* and other deciduous *Tamarix* drop their leaves and force *O. stactogalus* to overwinter in the egg stage within stems.

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